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Observations on *Eupelmus inyoensis* Girault (Hymenoptera: Eupelmidae)

L. E. Ehler and H. P. Sauter

Department of Entomology, University of California, Davis, California 95616

Abstract.—Eupelmus inyoensis Girault is a native, facultative secondary ectoparasite which has been reared from eight host species, representing six families and three orders of insects. This species is generally associated with the gall midge *Rhopalomyia californica* Felt on *Baccharis pilularis* DC in California; however, it is relatively rare and probably does not have a major impact on population dynamics of the midge. Analysis of galls containing *E. inyoensis* from the Jasper Ridge Biological Preserve and adjacent areas revealed that most contained only one individual of this species, regardless of the number of available hosts per gall. The evidence suggests that *E. inyoensis* has a relatively low reproductive capability; however, its broad host range and intrinsic competitive ability presumably enable it to persist in nature. Despite its rareness, this species appears well suited for coexistence in competitive parasite guilds.

Eupelmus inyoensis was described by Girault (1916) from specimens reared by Koebele from a dipterous gall on *Artemesia* at Inyo, California (Smith and Compere, 1928).[1] This native eupelmid is a solitary ectoparasite of various insect species and can develop as either a primary or secondary parasite, presumably depending on the host encountered. According to Burks (1979), it is known only from Utah and California. The literature on *E. inyoensis* is somewhat anecdotal and there is very little information on its field ecology. In the course of our investigations on the parasites of *Rhopalomyia californica* Felt in northern California, we accumulated a considerable amount of field data on *E. inyoensis*. The purpose of the present paper is to summarize this information. We also speculate on how this rather unusual parasitic species is able to persist in nature and coexist in competitive parasite guilds.

Host Range

Eupelmus inyoensis has been reared from eight host species, representing six families and three orders of insects (Table 1). These hosts represent both nonparasitic (phytophagous) and parasitic species, affirming that *E. inyoensis* is a

[1]According to G. A. P. Gibson (personal communication), current generic concepts in the Eupelmidae are unsatisfactory and most genera are in need of revision. When *Eupelmus* Dalman is revised, *E. inyoensis* Girault will be transferred to the genus *Brasema* Cameron. In view of this, we have deposited voucher specimens of our material at the following locations: Bohart Museum, University of California, Davis; U.S. National Museum, Washington, D.C.; and Biosystematics Research Center, Agriculture Canada, Ottawa.

Table 1. Hosts of *Eupelmus inyoensis*.

Order	*Family*	*Genus, species and authority*	*Reference*
Coleoptera	Bruchidae	*Bruchus* sp.	Smith and Compere (1928)
Diptera	Cecidomyiidae	*Rhopalomyia californica* Felt	Doutt (1961), Present paper
		Asphondylia adenostema Felt	Smith and Compere (1928)
Hymenoptera	Ichneumonidae	*Pimplopterus* sp.	Tilden (1951b, 1951c)
	Torymidae	*Torymus koebelei* (Huber)	Present paper
	Encyrtidae	*Metaphycus lounsburyi* (Howard)	Armitage (1923), Compere (1925), Smith and Compere (1928)
		Diversinervus smithi Compere[a]	Flanders (1952)
	Platygastridae	*Platygaster californica* (Ashmead)	Present paper

[a]Apparently not established in California.

facultative secondary parasite. The nonparasitic hosts include a bruchid and two cecidomyiids, and it is likely that other nonparasitic hosts exist in nature. The primary parasites exploited by *E. inyoensis* are associated with three host species: *Gnorimoschema baccharisella* Busck., a gall-forming gelechiid on *B. pilularis,* parasitized by *Pimplopterus* sp.; *R. californica,* parasitized by *T. koebelei* and *P. californica*; and *Saissetia oleae* (Olivier) (black scale), parasitized by *M. helvolus* and *D. smithi.* Black scale and its respective parasites are introduced and thus have no coevolutionary history with *E. inyoensis.* This is probably a conservative estimate of the host range because *E. inyoensis* may very well exploit other species in the respective guilds. For example, our records of secondary parasitization by *E. inyoensis* in the parasite guild associated with *R. californica* consist of those cases where the primary parasite could be identified with some degree of certainty; in many cases, *E. inyoensis* was observed parasitizing an immature parasite (of another species) whose identity could not be ascertained. It is also likely that *E. inyoensis* can parasitize other species in the parasite guild associated with black scale.

These findings suggest that facultative secondary parasites might be divided into two broad categories. There are species such as *E. inyoensis* which exploit more than one parasite guild (including nonparasitic hosts in some cases). Because black scale also occurs on *B. pilularis* (Kennett, 1986), *E. inyoensis* is capable of exploiting three different guilds, all on the same host plant. (Whether or not it parasitizes black scale and *G. baccharisella* has not been determined.) In contrast, other facultative species may be relatively "guild specific," exploiting only one phytophagous host and some or all of its primary parasites. *Zatropis capitis* Burks, a pteromalid ectoparasite in the guild associated with *R. californica,* may be an example.

Table 2. Frequency of *Eupelmus inyoensis* in dissected galls of *Rhopalomyia californica*.

Site	County	Date of collection	Subspecies of host	Galls Dissected Total	Galls Dissected With Eupelmus	Chambers Dissected Total	Chambers Dissected With Eupelmus
1	Yolo	24 Apr. 86	*consanguinea*	9	0	76	0
2	Solano	24 Apr. 86	*consanguinea*	10	0	123	0
3	Solano	21 May 86	*consanguinea*	12	6	143	14
4	Solano	28 July 86	*consanguinea*	13	9	151	34
5	Solano	7 Apr. 86	*pilularis*	19	0	209	0
6	Yolo	14 Apr. 86	*pilularis*	8	0	70	0
7	Yolo	6 Aug. 86	*pilularis*	10	1	128	1
				81	16	900	49

Frequency in Dissected Calls

Larvae of *R. californica* develop in terminal galls on both subspecies of *Baccharis pilularis* DC. The galls are usually multichambered, and can contain over 100 chambers per gall. Each chamber houses a single midge larva, along with whatever parasite progeny have been deposited therein. Additional aspects of the natural history and population ecology of the midge were given by Tilden (1951a), Doutt (1961), Force (1974), and Ehler (1982, 1987). In order to determine the frequency of occurrence for *E. inyoensis,* we collected galls from seven field sites during spring and summer of 1986. Four sites contained naturally occurring stands of ssp. *consanguinea* whereas the remaining three were urban plantings of ssp. *pilularis*. The sites containing ssp. *consanguinea* represented "endemic" midge populations (i.e., less than one gall per 100 terminals); the three urban sites displayed midge outbreaks (i.e., more than ten galls per 100 terminals). Overall, 81 galls were dissected. Of these, 16 (19.8%) contained at least one *E. inyoensis*; however, this species was present in only 49 of the 900 dissected chambers (Table 2). About 5% of the chambers were empty. Although parasitization by *E. inyoensis* was relatively high at site 4, the overall rate of parasitization was low (5.4%), and this is consistent with previous investigations (Doutt, 1961; Force, personal communication; Hopper, 1984; Ehler et al., 1984; Ehler, 1987).

At sites three and four, 48 chambers contained a total of 50 *E. inyoensis*. Of the 50, 17 occurred singly—i.e., developing as solitary primary parasites on midge larvae. Thirty occurred in chambers with other species of parasites—i.e., representing either multiple parasitization or hyperparasitization. The remaining 3 occurred in the same chamber with another species of parasite; this represents a case of both super- and multiple parasitization. No additional superparasitization was detected. Although preliminary, these data suggest that *E. inyoensis* shows little or no restraint with respect to multiple parasitization. (A possible exception involves hosts parasitized by *Torymus baccharidis* (Huber) [Force, personal communication]). In contrast, the data are consistent with a pattern of almost total restraint in the case of superparasitization. An alternative explanation for the latter pattern would be that ovipositing females simply do not have enough eggs immediately available to superparasitize. We also recognize that, in a relatively rare parasite, superparasitization could be virtually absent by random expectation alone. In any event, because *E. inyoensis* is a facultative secondary parasite, it would not be surprising to find that it does indeed avoid superparasitization, but not multiple parasitization.

Distribution of Progeny

Eupelmus inyoensis may be relatively rare in the field because it has a low capacity for increase. Although we were unable to test this hypothesis directly (i.e., by calculating r_c or r_m), we were able to assess indirect evidence which is consistent with the hypothesis. In a previous study, Ehler et al. (1984) collected over 3000 galls of *R. californica* at the Jasper Ridge Biological Preserve and the adjoining suburban areas of Woodside and Portola Valley. Galls were held in individual containers in the laboratory so that numbers of emerging midges and parasites could be recorded. *E. inyoensis* occurred in only 97 of 3023 galls (3.2%). This is probably a conservative estimate of actual occurrence because galls were removed prematurely from the field, and because there was usually some mortality of gall occupants in the laboratory. Nevertheless, the data again attest to the general rareness of *E. inyoensis* under natural field conditions.

The distribution of progeny was relatively consistent—i.e., an average of 1–2.5 *E. inyoensis* per exploited gall, regardless of the number of chambers (hosts) per gall (Figure 1). Although the regression in Figure 1 is significant, there is little slope to the regression line, and it is reasonable to assume that ovipositing females of *E. inyoensis* do not distribute their progeny in a manner which would result in a strong, direct-density dependent response. An inverse density-dependent response would be expected. The females evidently lack the reproductive capability to fully exploit the hosts in those galls in which they deposit progeny. For example, 71 of the 97 galls (73%) contained a single *E. inyoensis,* whereas 83 (85%) contained either one or two per gall. The highest number per gall was six ($n = 1$). Apparently, a large proportion of the exploited galls were exploited by only one ovipositing female. Statistical analysis of all 97 data points (as opposed to group means in Figure 1), gave essentially the same result as shown in the Figure, except for the expected lower coefficient of determination ($Y = 1.0271 + 0.0326X$, $r^2 = 0.08$, $P = 0.002$).

Discussion

In the parasite guild associated with *Rhopalomyia californica, Eupelmus inyoensis* is a relatively rare species. This is presumably due to a relatively low reproductive rate, as opposed to its being suppressed through interspecific competition or hyperparasitization. Nevertheless, this species is able to persist and this must be due in large measure to its flexible life style. As a facultative secondary parasite, *E. inyoensis* is a member of at least three parasite guilds associated with two native and one exotic phytophagous species on *Baccharis pilularis.* Within the guild associated with *R. californica,* it can develop as either a primary parasite of midge larvae, or as a secondary parasite of primary parasites such as *T. koebelei* and *P. californica.* In cases of multiple parasitization, it is evidently the superior competitor. (In this case, we would view hyperparasitization as "competition induced.") In the dissected galls, *E. inyoensis* was frequently observed parasitizing other parasite species, including older, more developed individuals. It may also avoid superparasitization, further

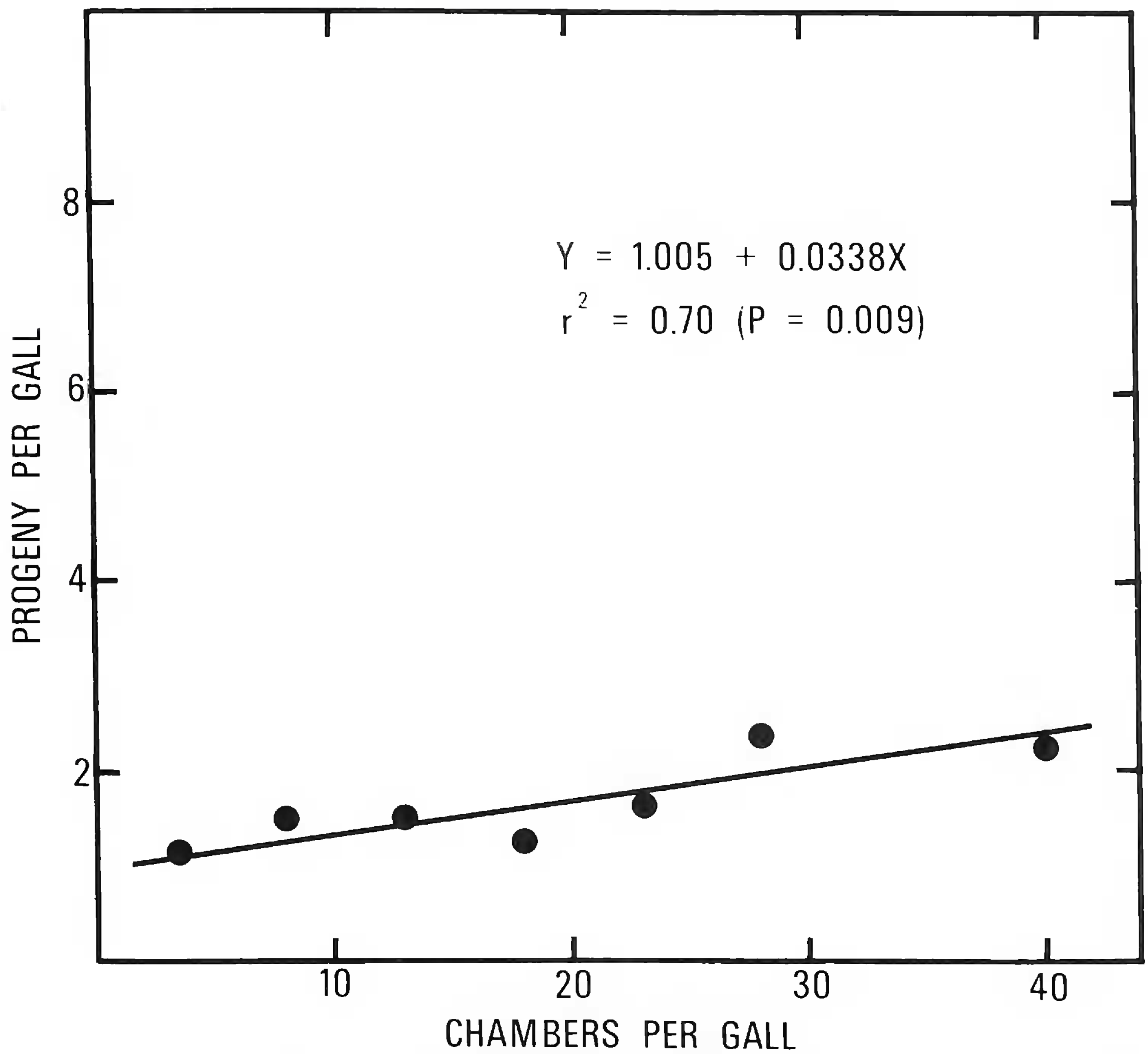

Figure 1. Mean number of *E. inyoensis* per gall as a function of number of hosts (chambers) per gall. Samples sizes (± SEM) for group means left to right: 11 (0.09), 23 (0.24), 19 (0.19), 19 (0.17), 9 (0.29), 9 (0.60), and 7 (0.60). Sample dates as given in Ehler et al. (1984) except for Woodside (only dates 4, 5, and 6).

enhancing the survival of its relatively few progeny. In summary, this rather unusual parasitic species appears well suited for coexistence in competitive parasite guilds.

The role of facultative secondary parasites in structuring parasite guilds is in need of investigation. In the case of *R. californica,* the parasite guild consists of over 10 species, but only seven are regularly collected throughout the host's range. Of the seven, three are facultative secondary parasites—i.e., *E. inyoensis, Z. capitis,* and an undescribed pteromalid in the genus *Mesopolobus.* The latter two can be relatively abundant at times. Primary parasites in the guild evidently do not oviposit in chambers containing either species (see Force, 1974). Also, evidence suggests that both *Z. capitis* and *Mesopolobus* preferentially parasitize certain primary parasites (Force, 1974; Hopper, 1984). Thus, these two species of facultative secondary parasites must have a considerable influence on the structure of the parasite guild. In contrast, *E. inyoensis* may have little influence on guild structure because it is so rare.

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